MORPHOLOGICAL CHANGES WITHIN THE CHAPARRAL VEGETATION TYPE AS RELATED TO ELEVATIONAL GRADIENTS

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Changes in vegetation structure with elevation on the lower slopes of the Sierra San Pedro Martir in Baja California have been described recently (Mooney and Harrison, 1972). It was found that at the lowest elevations the vegetation is a low scrub containing a high proportion of succulents. At somewhat higher elevations, this is replaced by a predominantly drought-deciduous scrub, coastal sage, and finally by an evergreen scrub chaparral. The vegetational trends accompanying these changes include an increase in plant density, an increase in the uniformity of heights of the dominant plants, and a change from predominantly drought-deciduous to predominantly evergreen elements. These ecological trends were interpreted in terms of adaptive responses to differences in moisture availability of the habitat.

The objective of the present study was to determine if similar adaptive clines could be identified within a single one of these physiognomically distinct vegetation types in the Sierra San Pedro Martir. In other words, how finely tuned are these adaptive systems?

The vegetation system chosen for study was the evergreen scrub community or chaparral. Samples were taken at three sites at approximately 500 m intervals representing the elevational extent of this type from its lowest representation near 700 m to near its upper reaches at 1800 m. The sites sampled, which were all on north-facing slopes, were all located along the road to the crest of the Sierra San Pedro Martir via the Melling Ranch. The road approximately parallels latitude 31° north. The sites were chosen on the basis of accessibility and a sufficiently uniform slope face to provide a relatively homogeneous sample area.

It can be assumed that soil water availability increases with elevation along this gradient. This follows simply from the fact of increased rainfall and decreasing temperature with elevation and from the characteristic summer drought throughout the gradient. The only climatic data available for this area are for San Telmo, a station located at 175 m elevation, which is below the base of the transect. At San Telmo average annual precipitation is 160 mm, the bulk of which falls in the winter (Hastings, 1964).

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At each site 18 to 20 ten-meter line intercept transects were taken by a random walk process from which the average percent cover of each woody species was determined. Each of these species was also scored for a number of morphological traits including presence or absence of such features as spines, strong leaf odor, and fissured bark. Qualitative estimates were made of the degree of leaf pubescence, leaf texture, and predominant leaf angle. Further, the leaves of each species were classified according to size. The average number of growing points per 20 centimeters of terminal branch (5 to 10 branches) were also noted. Finally, the maximum height encountered for each species was scored. All results given are expressed as a percentage of the ground cover that falls into a given class.

The possible functions of many of these traits such as spines, volatiles, and leaf size and texture have been discussed by Parsons (1973). Other traits such as bark characteristics were chosen because they are well-defined morphological traits and it was felt that inferences about their function might be made if clines were identified.

Results and Discussion

The three sampled sites had virtually identical total shrub cover (Table 1). Further, the heights of the woody plants were all predominantly in the 1 to 2 meter class (Table 2). Despite this general physiognomic similarity the species composition differed among the three stands. *Adenostoma fasciculatum* (chamise) and *Yucca schidigera* (Spanish bayonet) were the only two species encountered at all three sites. Adjacent sites, in each case, had over a third of their species in common. However, when percent cover is considered, the similarity between sites is somewhat less (Table 2).

In spite of the general physiognomic similarity of the various stands, there were a number of morphological features that varied systematically with elevation (Table 2). At the lowest and, presumably, driest site, approximately a quarter of the ground was covered by drought-deciduous shrubs. The evergreen elements became increasingly important with elevation and their leaf sizes larger. Coincident with increasing leaf size, vertically-oriented leaves become more prevalent and the leaves more sclerophytic. All of these trends can be related to the differences in water availability along the elevational gradient. At low elevations, where the drought is most severe, drought avoidance by leaf drop is the most important adaptive mode (Table 2). Where leaves are held only during periods of readily available moisture and relatively cool temperature, carbon gain is maximized with mesophytic leaves that can maintain high photosynthetic rates (Mooney and Dunn, 1970; Harrison et al., 1971). Even if leaf overtemperature (degrees of leaf temperature in excess of air temperature) occurs due to inefficient convective cooling, this may be beneficial, since air temperatures are relatively low during the late winter to early spring growing season. At the low eleva-

TABLE 1. PERCENT COVER OF THE PERENNIAL PLANTS ENCOUNTERED IN TRANSECT.

	Elevation in meters		
	760	1220	1830
Arctostaphylos bicolor (Nutt.) Gray	15.0		
Rhus laurina Nutt. in T. & G.	4.6		
Fraxinus trifoliata (Torr.) Lewis & Epling	4.2		
Cneoridium dumosum (Nutt.) Hook.	3.3		
Arctostaphylos oppositifolia Parry	3.0		
Lotus (cf. *scoparius*)	19.0		
Unknown shrub	0.8		
Haplopappus propinquus Blake	15.0	0.3	
Eriogonum fasciculatum Benth.	8.1	8.9	
Penstemon antirrhinoides Benth.	1.6	12.5	
Galium sp.	0.8	3.2	
Adenostoma fasciculatum H. & A.	14.0	1.8	8.1
Yucca schidigera Roezl.	0.5	0.8	0.9
Prunus ilicifolia (Nutt.) Walp.		9.6	
Rhamnus crocea Nutt. in T. & G.		5.0	
Adenostoma sparsifolium Torr.		4.9	
Artemisia tridentata Nutt.		1.6	
Ceanothus tomentosus Parry var. *olivaceus* Jeps.		1.4	
Ceanothus cuneatus (Hook.) Nutt.		1.1	
Arctostaphylos parryana Lemmon var. *pinetorum* (Roll.) Wies. & Schreib.		20.0	47.0
Garrya sp.		5.5	5.9
Heteromeles arbutifolia M. Roem.		5.3	0.7
Lonicera subspicata H. & A. var. *denudata* Rehid.		3.1	2.0
Rhus ovata S. Wats.		1.6	4.9
Quercus agrifolia Nee			7.4
Ceanothus leucodermis Greene			3.8
Ceanothus greggii Gray var. *perplexans* (Trel.) Jeps.			2.0
Rhamnus crocea Nutt. in T. & G. ssp. *ilicifolia* (Kell.) C. B. Wolf			1.3
Salix sp.			1.1
Opuntia sp.			0.6
Eriodictyon angustifolium Nutt.			0.6
Total % plant cover	89.9	86.6	86.3
Percent stand similarity			
Cover type basis	← 13 →	← 32 →	
Species basis	← 40 →	← 45 →	

tion drought-stressed end of the sclerophyll-gradient, the alternative strategy of being evergreen requires that the leaves be very small in order to avoid high leaf overtemperature during the summer months. During this period evaporative cooling by transpiration is strictly limited by low available moisture.

As summer water stress decreases, at higher elevations, evergreen sclerophylly increases (Table 2). Since photosynthesis can occur all year (Mooney and Dunn, 1970), the advantages of not having to replace an entire leaf crop each year, along with the continuous carbon gain during the summer may offset the advantages of the drought-deciduous

Table 2. Percent Woody Vegetation Ground Cover at Various Elevations Having the Following Features. (In certain instances it was not possible to score a particular species for a given feature. Thus the sum of the percentages of the various features does not always equal the total percent vegetation cover as given in Table 1.)

Feature	Elevation in Meters 760	1220	1830
Leaf texture			
Mesophytic	52.9	23.3	6.9
Intermediate	35.9	26.2	14.3
Sclerophytic	0.4	37.0	65.2
Leaf angle			
Vertical	6.3	34.4	56.7
Half vertical	2.9	21.3	7.1
Mixed	75.0	26.6	21.5
Horizontal	1.0	3.2	1.1
Leaf type			
Deciduous	25.7	12.5	0.0
Evergreen			
<26 mm^2	38.0	20.2	9.0
26 – 225 mm^2	3.2	10.7	9.0
226 – 1125 mm^2	23.2	35.3	60.7
1126 – 2025 mm^2	0.0	7.0	7.0
>2026 mm^2	0.0	1.0	0.5
Plant height, meters			
<0.5	0.0	0.0	0.0
0.51 – 1.0	0.9	1.1	2.2
1.01 – 1.5	46.6	13.6	5.6
1.51 – 2.0	6.2	31.6	55.9
>2.0	36.2	40.3	22.7
Growing points/20 cm branch			
1	0.5	0.8	1.6
2 – 10	37.5	29.5	16.0
11 – 20	32.0	47.9	66.8
21 – 30	3.3	0.0	2.0
31 – 100	0.9	8.1	0.0
Leaf pubescence			
None	69.3	64.3	74.7
Medium	19.0	19.0	11.7
Heavy	1.0	3.2	0.0
Leaf odor prevalent	18.3	1.9	2.6
Spiny	0.0	0.0	4.5
Fissured bark	46.1	28.2	10.1

shrubs that have high photosynthetic rates during the cool rainy season.

Leaves become larger and more sclerous as elevation and water availability increases. Cooler temperatures at high elevations reduce the probability of leaf overtemperature. The larger leaves confer a competitive advantage by intercepting more light from smaller, competing plants. They may also be more economical to make since it can be inferred that less stem tissue is needed to display a unit of photosynthetic tissue. With decreasing drought and heat stress, more leaves are maintained all year. Thus, there should be an increased advantage in maximizing carbon gain during as long a period as temperatures remain optimal for photosynthesis. The increased schlerophylly may reflect an adaptation to photosynthesis at low leaf water potentials later in the season. This adaptation may also be reflected in the increased emphasis on vertically oriented leaves at higher elevation. This orientation would reduce the radiant heat load on the leaves in the middle of the day when the sun's rays are also vertical. The lower leaf temperatures provided by vertical orientation may be especially important when stomata close during summer drought stress periods and evaporative cooling is nil.

Since upper leaves of such chaparral plants as *Heteromeles arbutifolia* are usually above photosaturation (Harrison, 1971), the vertical orientation probably does not significantly reduce carbon gain. Furthermore, it increases light penetration to lower leaves.

Certain morphological features, such as leaf pubescence and plant spininess, showed no strong changes along the elevational gradient. Other features, such as bark characteristics, leaf odor, and the number of growing points, did show distinctive trends (Table 2), the significance of which can only be speculative until experimental data are available.

The results of this survey indicate that there is considerable sorting of adaptive systems even within the climatic limits that circumscribe a single vegetation type. With additional physiological information, those aspects that relate to water and carbon balance of these systems could be quantitatively assessed to provide a model of fitness for any position along this environmental gradient.

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